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The effects of seafloor habitat complexity on survival of juvenile fishes: Species-specific interactions with structural refuge

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Abstract

Marine fishes are often associated with structurally complex microhabitats that are believed to provide a refuge from predation. However, the effects of habitat complexity on predator foraging success can be strongly modified by predator and prey behaviors. We conducted a series of laboratory experiments to evaluate the effects of sea floor habitat complexity on juvenile fish survivorship using multiple predator (striped searobin and summer flounder) and prey (winter flounder, scup, and black sea bass) species to identify potentially important species–habitat interactions. Three habitats of varying complexity (bare sand, shell, and sponge) common to coastal marine environments were simulated in large aquaria (2.4 m diameter, 2400 L volume). Prey survivorship increased significantly with greater habitat complexity for each species combination tested. However, examination of multiple prey and predator species across habitats revealed important effects of predator × habitat and prey × habitat interactions on prey survival, which appeared to be related to species-specific predator and prey behavior in complex habitats. Significant species × habitat interactions imply that the impact of reduced seafloor habitat complexity may be more severe for some species than others. Our results indicate that the general effects of seafloor habitat complexity on juvenile fish survivorship may be broadly applicable, but that the interaction of particular habitats with search tactics of predators as well as habitat affinities and avoidance responses of prey can produce differences among species that contribute to variable mortality.

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Keywords: Behavior; Foraging tactics; Habitat complexity; Juvenile survival; Mobile fishing gear; Prey vulnerability

1. Introduction

Many marine animals use structurally complex microhabitats such as shell debris, sand waves, burrows and depressions, cobble and gravel substrates, as well as biogenic structure provided by emergent epifaunal tubes, sponges, and patches of macroalgae and seagrass. Several fishes and invertebrates have been found distributed in non-random patterns and in close association with complex microhabitats in coastal and shelf marine environments (e.g., Auster et al., 1995; Levin and Hay, 1996; Hovel et al., 2002; Diaz et al., 2003). Juveniles often demonstrate particularly strong affinities for complex benthic habitats, which provide refuge from

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predation for young fishes (Lough et al., 1989; Able et al., 1995; Auster et al., 1997; Gregory and Anderson, 1997; Thrush et al., 2002).

Reduced availability of suitable habitat is being implicated increasingly as a factor causing declines or slowed recoveries in fish populations (e.g., Hutchings and Reynolds, 2004). The recognition of the importance of habitat, combined with implementations of holistic, ecosystem-based fishery management approaches, has generated hypotheses concerning the potential effects of mobile fishing gear (e.g., trawls and dredges) on complex seafloor habitats. These ideas have been summarized in several recent workshops and integrative publications (Auster et al., 1996; Jennings and Kaiser, 1998; Auster and Langton, 1999; Hall, 1999; Dayton et al., 2002; Johnson, 2002; Kaiser et al., 2002; National Research Council, 2002; Northeast Region Essential Fish Habitat Steering Committee, 2002; Chuenpagdee et al., 2003; Frid, 2003). Numerous field experiments have attempted to quantify changes in structural complexity of seafloor habitats and the organization of benthic communities in response to disturbance from bottom trawls and dredges (Thrush et al., 1995; Currie and Parry, 1996; Collie et al., 1997; Thrush et al., 1998; Freese et al., 1999; Turner et al., 1999; Thrush et al., 2001; Hermsen et al., 2003). These studies indicate that species composition and diversity changes as habitat complexity is reduced by disturbance from fishing gears. Since habitat recovery times can be longer than durations between fishing gear disturbance events, impacts on fish and invertebrate communities can represent permanent alterations (Thrush et al., 1995; Currie and Parry, 1996; Collie et al., 2000).

The most obvious benefit provided by a structurally complex seafloor is an increase in available predation refuge habitat. Complex habitat often provides absolute spatial refuges in the form of interstructural spaces within which small fishes are inaccessible to large-bodied predators. Laboratory experiments indicate that complex habitat features can interfere with predator search and pursuit behavior, contributing to lower predation vulnerability for small fishes occupying these habitats (Nelson and Bonsdorff, 1990; Gotceitas and Brown, 1993; Gotceitas et al., 1995; Fraser et al., 1996; Lindholm et al., 1999; Bartholomew et al., 2000; Ryer et al., 2004). Laboratory findings are supported by field studies that have documented a significant reduction in predation vulnerability for fishes using complex habitats (Tupper and Boutilier, 1995, 1997; Beukers and Jones, 1997; Heck et al., 2003). The effects of variable survivorship in juvenile fishes can have important consequences for population regulation (Steele, 1997; Caselle, 1999; Fromentin et al., 2001), and widespread reductions in the availability of structurally complex benthic habitats caused by mobile fishing gear disturbance could have significant indirect effects on recruitment success of many species.

Although structurally complex habitats generally enhance survivorship of young fishes, the extent to which survivorship is dependent on predator foraging and/or prey avoidance behaviors has not been thoroughly investigated. Tactics used for prey location and capture differ among predator species, as do the anti-predator responses of prey fishes. Predator and prey behaviors can interact with habitat complexity to determine the extent to which a particular habitat impairs predator search and capture or augments prey avoidance. To date, the few studies to investigate the role of species-specific behavior in potentially modifying the effect of habitat complexity have been limited to examinations of predator search behavior in vegetated habitats (Savino and Stein, 1989; Eklov and Diehl, 1994; McCollum, 1996), and a single study evaluating the effects of variable prey behavior among habitats (Ryer et al., 2004).

Here, we present results of experiments designed to evaluate the effects of variation in seafloor habitat complexity on the vulnerability of juvenile fishes to predation using multiple predator and prey species. Experiments used two predator species and three prey species common to US coastal waters of the Middle Atlantic Bight. To examine interactive effects of fish behavior and habitat complexity on juvenile fish survivorship, we chose predators with contrasting search and capture tactics and prey that demonstrate varying strengths of association with structured seafloor habitats.

2. Methods

2.1. Experimental animals

Predator and prey fishes were selected to maximize behavioral differences among species. Predators tested were summer flounder (*Paralichthys dentatus*) and striped searobin (*Prionotus evolans*). Summer flounder are visual predators that use slow stalking or ambush strike tactics (Olla et al., 1972; Manderson et al., 2000), while striped searobin employ an active search strategy that is believed to be largely dependent on pectoral fin rays modified for tactile and chemical reception to detect prey (Bardach and Case, 1965; Manderson et al., 1999). Prey species were juvenile stages of winter flounder (*Pseudopleuronectes americanus*), black sea bass (*Centropristis striata*), and scup (*Stenotomus chrysops*). Winter flounder are benthic flatfish that primarily use burial for predator avoidance (Manderson et al., 2000). Black sea bass are demersal and

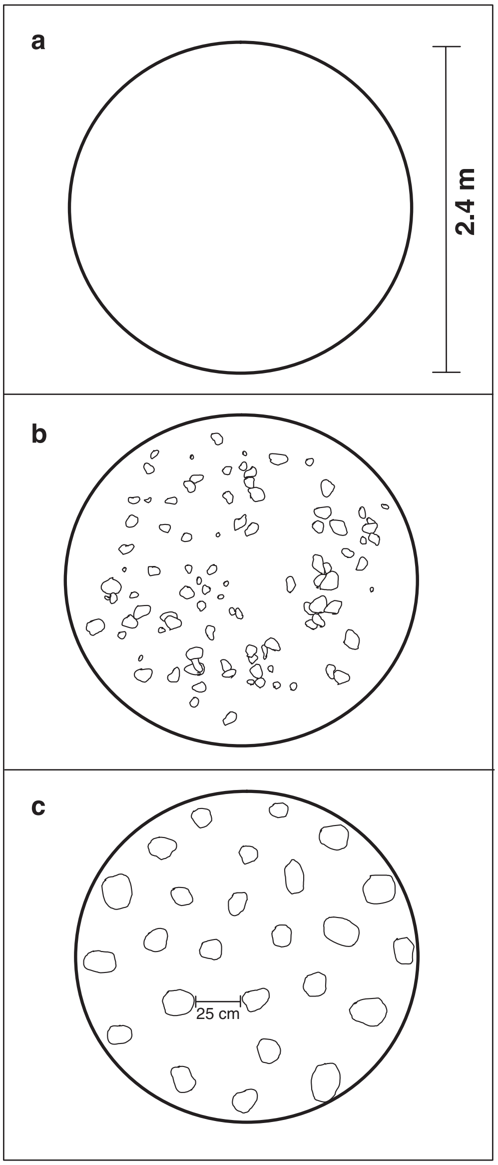

Fig. 1. Diagram of habitat treatments applied during laboratory experiments. (a) sand; (b) shell; (c) sponge. Drawings of shell and sponge treatments were reproduced from digital photographs and are approximately to scale.

demonstrate strong taxis for complex microhabitats (Able et al., 1995). Scup demonstrate pelagic schooling behavior and show the weakest affinity for benthic habitats (Able and Fahay, 1998). The juvenile stages of all three prey species are eaten by summer flounder and striped searobin predators in estuarine and coastal waters of the Middle Atlantic Bight (Manderson et al., 1999; Steimle et al., 1999; Manderson et al., 2000).

Predator (270–430 mm TL) and prey (37–75 mm TL) fishes were collected from Sandy Hook Bay, NJ (40°24′N, 74°00′W) during late spring and summer 2002. Predators were captured using barbless hook and line, and prey were captured using 1 m beam trawls, 4.9 m otter trawls, or 18 m beach seines. After transport to the laboratory, predators were maintained in 2400 L circular aquaria supplied with flow-through seawater at ambient temperatures (18–22 °C) and salinities (23–27 ppt), and were fed a combination of live and frozen fish prey ad libitum daily. Live fishes were included in predator diets to maintain natural foraging behavior in the laboratory. Predator populations were replenished periodically during the summer to provide naive individuals for experiments. Prey species were maintained in 1500 L circular aquaria or 475 L rectangular aquaria, supplied with flow-through ambient seawater, and fed live cultured brine shrimp, frozen clam, or a protein-rich commercial food (≤710 μm particle diameter) ad libitum daily.

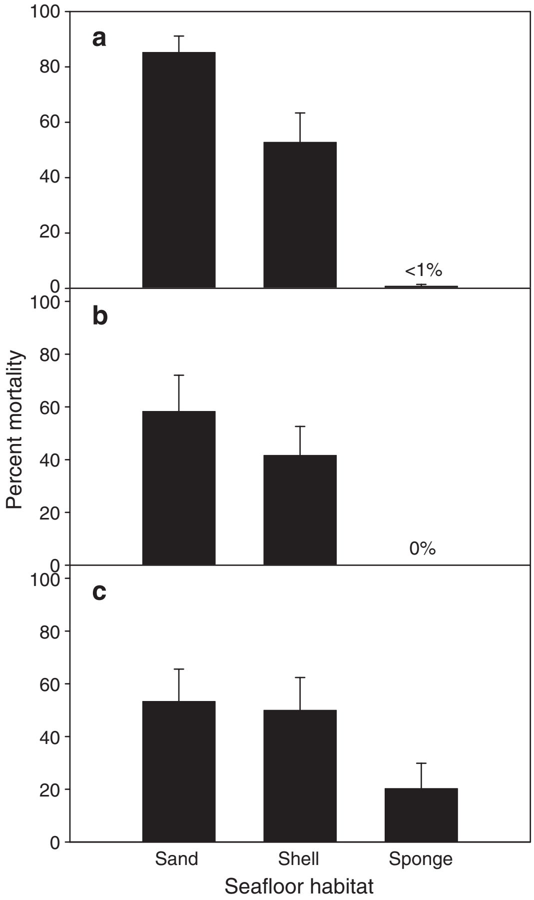

Fig. 2. Prey mortality by habitat treatment for striped searobin predators feeding on (a) winter flounder, (b) black sea bass, and (c) scup. Bars represent mean percent mortality ± 1 SE.

Table 1
Results of 2-factor fixed effects ANOVA testing the effects of prey species, habitat complexity, and the prey × habitat interaction on juvenile fish mortality

Source	Partial SS	*df*	MS	*F*	p
Model	67,128.12	8	8391.01	10.76	<0.001
Prey species	1706.78	2	853.39	1.09	0.339
Habitat treatment	43,033.44	2	21,516.72	27.59	<0.001
Prey × habitat	7537.99	4	1884.50	2.42	0.053
Error	81,119.01	104	779.99		
Total	148,247.13	112	1323.64		

2.2. Habitat treatments and experimental design

Experiments were conducted in nine 2400 L circular aquaria (2.4 m diameter × 0.6 m depth) identical to those used to maintain predator populations. All aquaria were supplied with a constant flow of ambient seawater and ~ 20 mm of medium grain sand (500 μm grain diameter) substrata. Aquaria were fitted with external drain pipes. Experimental treatments (Fig. 1) consisted of: (1) bare sand substrate that simulated a recently trawled seafloor; (2) sand substrate interspersed with patches of shell that simulated shell and shell debris habitats found in coastal environments; and (3) sand substrate with sponge that simulated structurally complex sponge species abundant in local waters (e.g., *Microciona prolifera*). Shell treatments consisted of partial or whole clam (*Mya* spp.) and oyster (*Crassostrea virginica*) shells (whole shell diameter = 6.5 cm) collected locally and placed haphazardly on the sand substrate. Sponge treatments consisted of various sizes (13–22 cm diameter) of natural sponge skeletons (*Spongia* or *Hippospongia* spp.) placed randomly with respect to size on the sand substrate. Each sponge was weighted with a small piece of galvanized steel attached to the sponge bottom to prevent predators from easily moving sponges along the substrate. Inter-sponge distances of 25 cm were maintained to allow predators to move freely between all sponges. Small inter-structural spacing relative to predator body size has been shown to interfere with predator movement and result in decreased foraging success (Bartholomew et al., 2000). Predator movements were also not inhibited by the arrangement of shell patches in the shell treatment. Our objective was to evaluate the effects of each refuge structure type on predation mortality rather than the effects of structure density or spatial arrangement. Substrate surface area (m^2) covered by shell and sponge habitat was maintained at 0.6 m^2 across and within treatments and represented ~ 15% bottom coverage in each aquarium (3.9 m^2 total available bottom surface area per aquarium). We considered bare sand to be the least complex treatment, the sponge treatment the most complex habitat, and the shell treatment intermediate in complexity based on differences in vertical relief provided by each habitat type.

For each replicate foraging trial, a single predator was measured for total length (TL), randomly placed into one of the experimental aquaria, and allowed to acclimate for 24 h. Prior to the initiation of each trial, predators were placed within opaque polyethylene flow-through enclosures (65–75 cm diameter) and 6–10 individual prey were measured (TL) and introduced to areas of aquaria outside the enclosures. Occasionally less than 10 prey were used in trials due to the difficulty in capturing sufficient numbers of prey in the field. After a one hour prey acclimation period, the enclosures were lifted and predators were allowed to feed for either 4 (striped

Table 2
Least significant difference contrasts examining the prey × habitat interaction

Effect of habitat treatment for each prey species

Prey species	Winter flounder		Scup		Black sea bass	
Contrast	Difference	*p*-value	Difference	*p*-value	Difference	*p*-value
Sand — sponge	84.4	<0.001	33.0	0.030	58.3	<0.001
Shell — sponge	52.0	<0.001	29.6	0.050	41.7	0.009
Sand — shell	32.4	0.006	3.4	0.856	16.6	0.326

Effect of prey species within each habitat treatment

Habitat treatment	Sand		Shell		Sponge	
Contrast	Difference	*p*-value	Difference	*p*-value	Difference	*p*-value
WF — scup	31.9	0.009	2.9	0.771	− 19.5	0.090
WF — bass	26.9	0.061	11.1	0.565	0.8	0.904
Scup — bass	− 5.0	0.548	8.2	0.774	20.3	0.178

Differences are between treatment means (% mortality). WF = winter flounder.

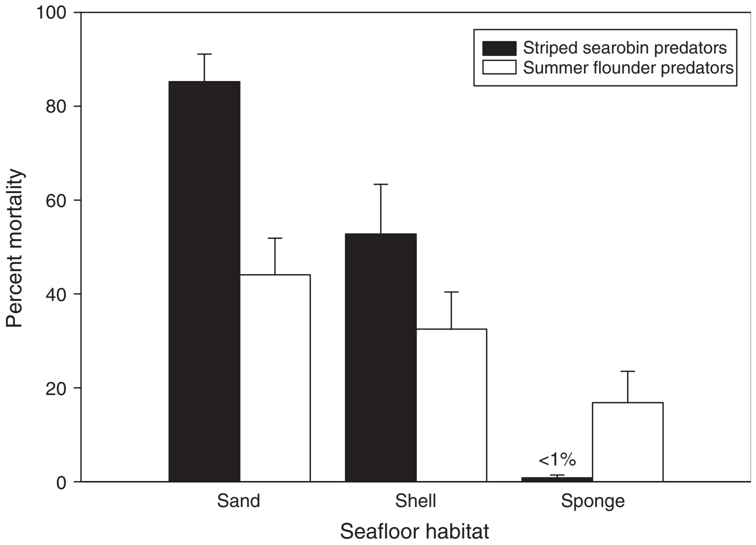

Fig. 3. Mortality of winter flounder prey by habitat treatment for striped searobin and summer flounder predators. Bars represent mean percent mortality ± 1 SE.

searobin predators) or 24 (summer flounder predators) hours. Examination of striped searobin and summer flounder consumption rates during previous experimental studies (Manderson et al., 1999, 2000) indicated that the number of prey fishes eaten was roughly equivalent using 4 and 24 h feeding periods, respectively. Maintaining comparable overall prey consumption between predators ensured that habitat × predator species interactions would be minimally affected by any differences between predators in physiological feeding requirements and, instead, be mainly due to behavioral differences. After the feeding period, predators were removed, water levels were lowered, and surviving prey were located and counted.

To control for variable size-dependent capture success, prey/predator size ratios were maintained between 15% and 25%. These represented low to moderate size ratios when compared to the relative prey sizes consumed by striped searobin and summer flounder in previous studies (Manderson et al., 1999, 2000). As a result, absolute prey and predator sizes varied slightly among species. Summer flounder predators (=373.8 mm TL) were larger ($F=177.8$; $p<0.001$) than striped searobin predators (=321.1 mm TL), and, thus, prey sizes also differed ($F=198.6$; $p<0.001$) among species (winter flounder = 54.7 mm TL; scup = 50.1 mm TL; black sea bass = 64.0 mm TL) to maintain prey/predator size ratios. However, for each predator and prey species combination tested, no significant differences existed in predator size ($F=0.22$; $p=0.80$) or prey size ($F=0.33$; $p=0.72$) among habitat treatments.

Initial experiments were performed to evaluate the effects of the strength of prey association with structure on prey mortality by offering each of three prey species: winter flounder, black sea bass, and scup to striped searobin predators. Based on the outcome of these feeding trials, an additional series of experiments was then conducted offering winter flounder prey to summer flounder predators to examine the effects on prey mortality of differences in predator search strategy. Difficulty in capturing sufficient numbers of suitably sized prey species in the field prohibited us from performing experiments with summer flounder predators and each of three prey species. We selected winter flounder prey for this comparison due to availability and because winter flounder was the only prey species to demonstrate significant differences in mortality across all habitat complexity treatments during feeding trials with striped searobin predators (see Results).

Percent mortality of prey was calculated for each experimental feeding trial and normalized using an arcsine

Table 3
Results of 2-factor fixed effects ANOVA testing the effects of predator species, habitat complexity, and the predator × habitat interaction on winter flounder mortality

Source	Partial SS	*df*	MS	*F*	p
Model	56,916.04	5	11,383.21	16.95	<0.001
Predator species	3986.57	1	3986.57	5.94	0.017
Habitat treatment	42,247.71	2	21,123.86	31.45	<0.001
Predator × habitat	12,426.59	2	6213.29	9.25	<0.001
Error	69,847.33	104	671.61		
Total	126,763.37	109	1162.97		

Table 4
Least significant difference contrasts examining the predator × habitat interaction

Effect of habitat treatment for each predator species

Predator species	Striped searobin		Summer flounder	
Contrast	Difference	p-value	Difference	p-value
Sand — sponge	84.4	<0.001	27.2	0.013
Shell — sponge	52.0	<0.006	15.6	0.134
Sand — shell	32.4	0.003	11.6	0.309

Effect of predator species within each habitat treatment

Habitat treatment	Sand		Shell		Sponge	
Contrast	Difference	p-value	Difference	p-value	Difference	p-value
SSR — SF	41.1	<0.001	20.3	0.059	−16.1	0.054

Differences are between treatment means (% mortality). SSR = striped searobin; SF = summer flounder.

square root transformation (Shapiro–Wilk test for normality, $p=0.154$ after transformation). The data were then analyzed using fixed effects ANOVA models. Prey species, habitat complexity, and their interaction were assessed with a 2-factor ANOVA model, testing for differences in mortality among the three habitat treatments for each of the three prey species when offered to striped searobin predators. The effects of predator species, habitat complexity, and their interaction were also assessed with a 2-factor ANOVA model, testing for differences in winter flounder mortality among the three habitat treatments when offered to each of the two predator species. Post-hoc contrast analyses were completed where appropriate using an experiment-wise error rate of 0.05. Since the number of prey individuals was occasionally less than 10 in some trials, we also used the same ANOVA models to test for differences in the number of prey consumed, rather than percent mortality. The results were not different and thus, only the results for percent mortality are presented.

3. Results

A total of 167 feeding trials was completed to evaluate how juvenile fish mortality is influenced by the interaction between predator and prey species and habitat complexity. The effect of habitat complexity on prey mortality was dependent on prey species (Fig. 2, Table 1) in the experiments with striped searobin predators. Winter flounder experienced differential mortality among all habitat treatments, while mortality of scup and black sea bass was not different between the sand and shell habitats (Fig. 2, Table 2). Winter flounder prey experienced higher mortality (=85.2%) than scup (=53.3%) and black sea bass (=58.3%) in sand habitat, whereas no appreciable difference in mortality was observed between scup and black sea bass in sand (Fig. 2, Table 2). In shell habitat, mortality was similar among the three prey species (winter flounder=52.8%; scup=49.9%; black sea bass=41.7%) (Fig. 2, Table 2). In sponge habitat, however, scup experienced higher mortality (=20.3%) compared to winter flounder (=0.8%) and black sea bass (=0.0%) (Fig. 2, Table 2).

Variation in winter flounder mortality among habitat complexity treatments was also dependent on predator species (Fig. 3, Table 3). Mortality rates of winter flounder were significantly different in all habitats when offered to striped searobin predators, but only demonstrated considerable differences between sand and sponge habitats when exposed to summer flounder predators (Table 4). In sand and shell habitats, mortality of winter flounder was higher when exposed to striped searobin compared to summer flounder predators (sand habitat: striped searobin=85.2%; summer flounder=44.1%; shell habitat: striped searobin=52.8%; summer flounder =32.5%) (Fig. 3, Table 4). The pattern was reversed in sponge habitats, in which summer flounder caused higher winter flounder mortality than striped searobin (summer flounder=16.9%; striped searobin=0.8%) (Fig. 3, Table 4). Although the statistical significance of some the pairwise contrasts was marginal ($0.05<p<0.10$; Tables 2 and 4), we maintain that differences in mortality between treatment means ranging from 16.1% to 26.9% are biologically meaningful.

4. Discussion

4.1. Structural complexity and prey vulnerability

We detected a strong positive effect of increased habitat complexity on prey survivorship. Across each predator and prey species combination examined, high vertical relief sponge habitat provided the greatest survival benefit, while prey mortality was highest in unstructured sand habitat. Complex habitats provide a spatial refuge for potential prey organisms resulting in increased survivorship when compared with unstructured habitats. The generality of this phenomenon in aquatic systems is supported by numerous field and laboratory studies of fishes and invertebrates comparing a variety of microhabitats (Orth et al., 1984; Main, 1987; Gotceitas et al., 1995; Tupper and Boutilier, 1995, 1997; Lindholm et al., 1999; Manderson et al., 2000; Wennhage, 2002; Ryer et al., 2004).

Prey vulnerability to predation can be viewed as the product of two components: (1) the probability of encounter and (2) the susceptibility to capture (Greene, 1986). Complex seafloor habitats can influence each component of prey vulnerability by lowering encounter probability or by interfering with pursuit and capture subsequent to encounter. Reduced encounter probabilities in complex habitats have been observed to result from habitat effects on both predator searching behavior and detection ability. For example, Ryer et al. (2004) found lower encounter rates in sponge compared with sand habitat for Pacific halibut predators. Since the frequency of pursuits by halibut predators was not different between sponge and sand habitats, the authors attributed reduced encounters to slower predator search speeds as well as a reduction in the total area searched in sponge habitat, but not to lowered detection capabilities. Lindholm et al. (1999) observed a decline in the reaction distance of Atlantic cod predators with increasing habitat complexity and concluded that predator detection capabilities were impaired by high density structure, resulting in a reduced number of prey encounters.

The relationship between predator body size and the spacing between habitat structural components may affect movements and search patterns of mobile predators (Bartholomew et al., 2000). We maintained approximately equal spacing (25 cm) between adjacent sponges to allow easy passage among sponges by predators (searobin: length = 32.1 cm, depth/width = 10 cm; summer flounder: length = 37.4 cm, depth/width = 15 cm). The maintenance of sufficiently large inter-structural spacing minimized the negative effects of sponge habitat on predator search ability since our other habitat treatments (sand, shell) did not impair predator search behavior. Therefore, in our experiments, habitat complexity provided by shell and sponge probably decreased the detectibility of prey to predators rather than impaired predator search behaviors. For example, black sea bass avoided predator detection by occupying small openings within sponges and crevices between and under shells (FS Scharf, personal and video observation).

Prey vulnerability to predation is also determined by post-encounter processes including pursuit, capture, and ingestion. High vertical relief habitat can reduce predation efficiency by impeding the pursuit of predators that rely on high swimming velocities to capture prey. Ryer et al. (2004) observed reduced capture success in sponge habitat compared with sand habitat and attributed this pattern to the frequent loss of predator visual contact with prey moving among sponges during chases. Other studies that examined behavior directly have also concluded that increased habitat complexity reduces post-encounter capture efficiency by restricting predator pursuit and interrupting predator visual fields, allowing prey individuals to redistribute within the structured habitat and avoid further detection (Savino and Stein, 1982; Main, 1987; Christensen and Persson, 1993). The structured habitats (shell and sponge) used in our experiments probably affected the pursuit of detected prey in a stepwise manner, with sponge habitat creating the greatest obstruction to predator capture behavior. In addition to negatively affecting predator pursuit and capture, habitat complexity can lower the probability of attack upon encounter if prey can utilize protective spaces. Ryer (1988) proposed that small amphipods avoided attacks by large pipefish by using the base of grassblades to maintain sufficient distance from predators. In our study, black sea bass were often found occupying spaces under shells and within sponges, and winter flounder were frequently found partially buried in the sediment directly under sponges. Therefore, in addition to reducing the probability of prey detection, the use of small crevices within structured habitat may have lowered attack rates on those prey individuals that were detected.

4.2. Interactive effects of habitat complexity and behavior

Although all prey species realized higher survival as habitat complexity increased in our experiments, we detected an interactive effect of prey species and habitat type on prey mortality. Contrary to expectations, we observed higher mortality for winter flounder on bare sand substrata compared to black sea bass and scup. Flatfishes typically use complete or partial burial and crypsis to avoid detection by predators, which should enable flatfishes to better utilize the sediment as a refuge compared to fusiform fishes. However, striped searobin are particularly well adapted for locating potential prey at or just beneath the sediment surface via mechanical and chemical reception associated with pectoral fin rays (Bardach and Case, 1965). In laboratory observations, Manderson et al. (1999) found that striped searobin were effective at causing juvenile winter flounder prey to flush from the sediment and were successful in nearly two-thirds of attacks. Our results indicate that, if detected by a predator with appropriate sensory reception, the evasive abilities of winter flounder are low and that, relative to black sea bass and scup, their vulnerability to certain predators can be high despite the availability of a sediment refuge.

The high relief sponge habitat also generated differential mortality among prey species. Only scup, the species with the weakest affinity for structured, benthic habitats, suffered appreciable mortality in sponge habitat (>20%). Striped searobin were unable to forage effectively on demersal, structure-oriented (black sea bass) or benthic, cryptic (winter flounder) prey species (<1% for each species) in high vertical relief habitat. These patterns indicate that susceptibility to detection and/or capture by an actively searching predator was considerably lower for prey fishes associated with the substrate, below the top of the high relief sponge habitat, compared to a pelagic-oriented species that primarily forms shoals as a defensive behavior. In a study of two flatfish species, Ryer et al. (2004) found that halibut prey reduced their flight response in complex sponge habitat compared to sand habitat, resulting in significantly lower encounter rates with predators. In the same study, the more cryptic rock sole appeared to rely mostly on burial to avoid detection, and encounter rates with predators did not differ significantly between habitat types (Ryer et al., 2004). Our results provide further evidence of the important interaction between habitat and species-specific behavior of prey in determining the refuge value of complex habitats.

Prey survivorship was also dependent on interactions between predator species and habitat type. In low relief habitats (sand, shell) actively searching striped searobin predators caused higher mortality for winter flounder prey than summer flounder predators. However, summer flounder predators caused higher mortality in high relief sponge habitat. This finding suggests that the high relief sponge habitat impeded search and/or pursuit to a much larger extent for an actively searching predator (striped searobin) than for a predator (summer flounder) that employs slow stalking or ambush foraging tactics. Similar results, demonstrating reduced effects of habitat complexity on predators adopting ‘sit and wait’ behavior, have been found for pike (Savino and Stein, 1989; Eklov and Diehl, 1994), southern flounder (McCollum, 1996), and lined seahorses (James and Heck, 1994). Furthermore, several predators, including largemouth bass (Savino and Stein, 1989), perch (Eklov and Diehl, 1994), as well as lined seahorses (James and Heck, 1994), have been observed to shift foraging behavior from actively searching to ambush tactics when prey occupy complex habitats. However, we did observe a monotonic decrease in prey mortality across habitat types (sand > shell > sponge) for summer flounder predators, unlike other studies that found no effects of habitat complexity on the foraging rates of an ambush predator (James and Heck, 1994; McCollum, 1996). We attribute this to the fact that summer flounder are not obligate ambush predators and have been observed to use slow stalking tactics (Olla et al., 1972; Manderson et al., 2000).

5. Conclusions

Our results may have important implications for the identification of essential fish habitats and the management and conservation of marine ecosystems. We have reinforced the evidence supporting the importance of complex habitats for juvenile fish survivorship and provided new evidence of significant interactions between both predator and prey species and habitat. The strong association between many species of marine juvenile fishes and structured habitat is well documented (Auster et al., 1995; Thrush et al., 2002; Diaz et al., 2003). In heavily trawled or dredged areas, reductions in physical (e.g., bedforms) and biogenic structure appear to be common (Thrush et al., 1998; Freese et al., 1999), with coincident declines in biodiversity, abundance, and production of benthic fauna (Thrush et al., 2001; Hermsen et al., 2003). Moreover, many structured habitats disturbed by mobile fishing gear have slow recovery rates and may remain in a constant altered state if the frequency of fishing is relatively high (Collie et al., 2000). The designation of marine sanctuaries or protected areas as a fisheries management tool in addition to traditional catch and effort restrictions holds promise for the conservation of important juvenile habitats. Lindholm et al. (2001) explicitly incorporated habitat complexity into a population model for Atlantic cod in the Gulf of Maine and predicted a strong linear relationship between the habitat area closed to mobile fishing gear and juvenile fish survival. We conclude that, although our findings indicate that variation in survivorship will be specific for each predator–prey–habitat association, increased availability of complex seafloor habitat will benefit most benthic and demersal marine species through higher juvenile survival and may help to alleviate habitat-related recruitment bottlenecks.

Clearly, the effects of reduced seafloor complexity related to mobile fishing gears will not be similar among juvenile fish taxa. Behavioral tactics used by predators and prey can offset the function of complex habitat and may also operate synergistically with specific habitats to modify the foraging process. Knowledge of species life history, behavior, and ecology will be critical for understanding how structured habitats contribute to juvenile survival and ultimately to variable population dynamics. Future studies should continue to examine habitat-specific survivorship for well known trophic linkages in order to uncover strong interactions and identify those species that may be most affected by reductions in habitat complexity.

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References

Able, K.W., Fahay, M.P., 1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick NJ. 342 pp.

Able, K.W., Fahay, M.P., Shepherd, G.R., 1995. Early life history of black sea bass, *Centropristis striata*, in the mid-Atlantic Bight and a New Jersey estuary. Fish. Bull. 93, 429–445.

Auster, P.J., Langton, R.W., 1999. The effects of fishing on fish habitat. In: Benaka, L. (Ed.), Fish Habitat: Essential Fish Habitat (EFH) and Rehabilitation. American Fisheries Society, Bethesda MD, pp. 150–187.

Auster, P.J., Malatesta, R.J., LaRosa, S.C., 1995. Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. Mar. Ecol. Prog. Ser. 127, 77–85.

Auster, P.J., Malatesta, R.J., Donaldson, C.L.S., 1997. Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. Environ. Biol. Fish. 50, 195–200.

Auster, P.J., Malatesta, R.J., Langton, R.W., Watling, L., Valentine, P.C., Donaldson, C.L.S., Langton, E.W., Shepard, A.N., Babb, I. G., 1996. The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): implications for conservation of fish populations. Rev. Fish. Sci. 4, 185–202.

Bardach, J.E., Case, J., 1965. Sensory capabilities of the modified fins of squirrel hake (*Urophycis chuss*) and searobins (*Prionotus carolinus* and *P. evolans*). Copeia 2, 194–206.

Bartholomew, A., Diaz, R.J., Cicchetti, G., 2000. New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. Mar. Ecol. Prog. Ser. 206, 45–58.

Beukers, J.S., Jones, G.P., 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114, 50–59.

Caselle, J.E., 1999. Early post-settlement mortality in a coral reef fish and its effect on local population size. Ecol. Monogr. 69, 177–194.

Christensen, B., Persson, L., 1993. Species-specific antipredatory behaviours: effects on prey choice in different habitats. Behav. Ecol. Sociobiol. 32, 1–9.

Chuenpagdee, R., Morgan, L.E., Maxwell, S.M., Norse, E.A., Pauly, D., 2003. Shifting gears: assessing collateral impacts of fishing methods in US waters. Front. Ecol. Environ. 1, 517–524.

Collie, J.S., Escanero, G.A., Valentine, P.C., 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. Mar. Ecol. Prog. Ser. 155, 159–172.

Collie, J.S., Hall, S.J., Kaiser, M.J., Poiner, I.R., 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. J. Anim. Ecol. 69, 785–798.

Currie, D.R., Parry, G.D., 1996. Effects of scallop dredging on a soft sediment community: a large-scale experimental study. Mar. Ecol. Prog. Ser. 134, 131–150.

Dayton, P.K., Thrush, S., Coleman, F.C., 2002. Ecological effects of fishing in marine ecosystems of the United States. Pew Oceans Commission, Arlington, VA, p. 44.

Diaz, R.J., Cutter, G.R., Able, K.W., 2003. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 26, 12–20.

Eklov, P., Diehl, S., 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. Oecologia 98, 344–353.

Fraser, S., Gotceitas, V., Brown, J.A., 1996. Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Can. J. Fish. Aquat. Sci. 53, 305–314.

Freese, L., Auster, P.J., Heifetz, J., Wing, B.L., 1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Mar. Ecol. Prog. Ser. 182, 119–126.

Frid, C.L.J., 2003. Managing the health of the seafloor. Front. Ecol. Environ. 1, 429–436.

Fromentin, J., Myers, R.A., Bjornstad, O.N., Stenseth, N.C., Gjosaeter, J., Christie, H., 2001. Effects of density-dependent and stochastic processes on the regulation of cod populations. Ecology 82, 567–579.

Gotceitas, V., Brown, J.A., 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia 93, 31–37.

Gotceitas, V., Fraser, S., Brown, J.A., 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Mar. Biol. 123, 421–430.

Greene, C.H., 1986. Patterns of prey selection: implications of predator foraging tactics. Am. Nat. 128, 824–839.

Gregory, R.S., Anderson, J.T., 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Mar. Ecol. Prog. Ser. 146, 9–20.

Hall, S.J., 1999. The effects of fishing on marine ecosystems and communities. Blackwell Science, Osney Mead OX. 296 pp.

Heck, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser. 253, 123–136.

Hermsen, J.M., Collie, J.S., Valentine, P.C., 2003. Mobile fishing gear reduces benthic megafaunal production on Georges Bank. Mar. Ecol. Prog. Ser. 260, 97–108.

Hovel, K.A., Fonseca, M.S., Myer, D.L., Kenworthy, W.J., Whitfield, P.E., 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. Mar. Ecol. Prog. Ser. 243, 11–24.

Hutchings, J.A., Reynolds, J.D., 2004. Marine fish population collapses: consequences for recovery and extinction risk. BioScience 54, 297–309.

James, P.L., Heck Jr., K.L., 1994. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. J. Exp. Mar. Biol. Ecol. 176, 187–200.

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34, 202–352.

Johnson, K.A., 2002. A review of national and international literature on the effects of fishing on benthic habitats. U.S. Department of Commerce. 72 pp.

Kaiser, M.J., Collie, J.S., Hall, S.J., Jennings, S., Poiner, I.R., 2002. Modification of marine habitats by trawling activities: prognosis and solutions. Fish and Fish. 3, 114–136.

Levin, P.S., Hay, M.E., 1996. Responses of temperate reef fishes to alterations in algal structure and species composition. Mar. Ecol. Prog. Ser. 134, 37–47.

Lindholm, J.B., Auster, P.J., Kaufman, L.S., 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 180, 247–255.

Lindholm, J.B., Auster, P.J., Ruth, M., Kaufman, L., 2001. Modeling the effects of fishing and implications for the design of marine protected areas: juvenile fish responses to variations in seafloor habitat. Conserv. Biol. 15, 424–437.

Lough, R.G., Valentine, P.C., Potter, D.C., Auditore, P.J., Bolz, G.R., Neilson, J.D., Perry, R.I., 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Mar. Ecol. Prog. Ser. 56, 1–12.

Main, K.L., 1987. Predator avoidance in seagrass meadows: prey behavior, microhabitat selection, and cryptic coloration. Ecology 68, 170–180.

Manderson, J.P., Phelan, B.A., Stoner, A.W., Hilbert, J., 2000. Predator–prey relations between age-1+ summer flounder (*Paralichthys dentatus*, Linnaeus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. J. Exp. Mar. Biol. Ecol. 251, 17–39.

Manderson, J.P., Phelan, B.A., Bejda, A.J., Stehlik, L.L., Stoner, A.W., 1999. Predation by striped searobin (*Prionotus evolans*, Triglidae) on young-of-the-year winter flounder (*Pseudopleuronectes americanus*, Walbaum): examining prey size selection and prey choice using field observations and laboratory experiments. J. Exp. Mar. Biol. Ecol. 242, 211–231.

McCollum, B.R., 1996. Effects of physical and visual habitat complexity on predation by active and ambush piscivores: experimental tests with bluefish and southern flounder preying on spot. Department of Zoology. North Carolina State University, Raleigh, p. 39.

National Research Council, 2002. Effects of trawling and dredging on seafloor habitat. National Academy of Sciences, Washington, DC.

Nelson, W.G., Bonsdorff, E., 1990. Fish predation and habitat complexity: are complexity thresholds real? J. Exp. Mar. Biol. Ecol. 141, 183–194.

Northeast Region Essential Fish Habitat Steering Committee, 2002. Workshop on the effects of fishing gear on marine habitats off the Northeastern United States, October 23–25, 2001, Boston, Massachusetts. Northeast Fisheries Science Center Reference Document 02-01. U.S. Dept. of Commerce, Woods Hole, MA.

Olla, B.L., Samet, C.E., Studholme, A.L., 1972. Activity and feeding behavior of the summer flounder (*Paralichthys dentatus*) under controlled laboratory conditions. Fish. Bull. 70, 1127–1136.

Orth, R.J., Heck Jr., K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. Estuaries 7, 339–350.

Ryer, C.H., 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. Mar. Ecol. Prog. Ser. 48, 37–45.

Ryer, C.H., Stoner, A.W., Titgen, R.H., 2004. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. Mar. Ecol. Prog. Ser. 268, 231–243.

Savino, J.F., Stein, R.A., 1982. Predator–prey interactions between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Trans. Am. Fish. Soc. 111, 255–266.

Savino, J.F., Stein, R.A., 1989. Behavioural interactions between fish predators and their prey: effects of plant density. Anim. Behav. 37, 311–321.

Steele, M.A., 1997. Population regulation by post-settlement mortality in two temperate reef fishes. Oecologia 112, 64–74.

Steimle, F.W., Zetlin, C.A., Berrien, P.L., Chang, S., 1999. Essential fish habitat source document: Black sea bass, *Centropristis striata*, life history and habitat characteristics.

Thrush, S.F., Hewitt, J.E., Cummings, V.J., Dayton, P.K., 1995. The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? Mar. Ecol. Prog. Ser. 129, 141–150.

Thrush, S.F., Schultz, D., Hewitt, J.E., Talley, D., 2002. Habitat structure in soft-sediment environments and abundance of juvenile snapper *Pagrus auratus*. Mar. Ecol. Prog. Ser. 245, 273–280.

Thrush, S.F., Hewitt, J.E., Funnell, G.A., Cummings, V.J., Ellis, J., Schultz, D., Talley, D., Norkko, A., 2001. Fishing disturbance and marine biodiversity: role of habitat structure in simple soft-sediment systems. Mar. Ecol. Prog. Ser. 221, 255–264.

Thrush, S.F., Hewitt, J.E., Cummings, V.J., Dayton, P.K., Cryer, M., Turner, S.J., Funnell, G.A., Budd, R.G., Milburn, C.J., Wilkinson, M.R., 1998. Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. Ecol. Appl. 8, 866–879.

Tupper, M., Boutilier, R.G., 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 52, 1834–1841.

Tupper, M., Boutilier, R.G., 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Mar. Ecol. Prog. Ser. 151, 225–236.

Turner, S.J., Thrush, S.F., Hewitt, J.E., Cummings, V.J., Funnell, G., 1999. Fishing impacts and the degradation or loss of habitat structure. Fisheries Manag. Ecol. 6, 401–420.

Wennhage, H., 2002. Vulnerability of newly settled plaice (*Pleuronectes platessa* L.) to predation: effects of habitat structure and predator functional response. J. Exp. Mar. Biol. Ecol. 269, 129–145.